

Mass Extinction in a Simple Mathematical Biological Model

Kei Tokita*

Department of Chemistry and Chemical Biology, Harvard University, 12 Oxford Street, Cambridge MA 02138

Ayumu Yasutomi

Suntory and Toyota International Centres for Economics and Related Disciplines
London School of Economics and Political Science, London WC2A 2AE, UK

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Introducing the effect of extinction into the so-called replicator equations in mathematical biology, we construct a general model of ecosystems. The present model shows mass extinction by its own *extinction dynamics* when the system initially has a large number of species (*diversity*). The extinction dynamics shows several significant features such as a power law in basin size distribution, induction time, etc. The present theory can be a mathematical foundation of the *species-area effect* in the paleontologic theory for mass extinction.

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Mechanisms of mass extinction of species in ecosystems have been studied by a number of researchers [1,2]. Their conclusions can be divided into two categories, one emphasizing exogenous shocks [3–6] and the other, endogenous causes [7–9]. Building on both views, we construct a general mathematical biological model of ecosystems. This model reflects the former view, e.g., the situation where several biotas which have been separated from each other for a long time are suddenly integrated into a larger ecological network (biotic fusion) by some exogenous shock [10,11]. We assume that the interaction coefficients for this newly produced ecosystem can be written in the form of a random matrix [12–15]. Also, following the latter view, we adopt the concept of an ‘extinction threshold’, which we introduce into the replicator equations [16] of population dynamics. Using this replicator equation model with random interaction and the extinction threshold, we find several significant new features characterizing the nature of mass extinction.

We investigate the following N_I dimensional ordinary differential equations:

$$\frac{dx_i(t)}{dt} = x_i(t) \left(\sum_{j=1}^{N_I} a_{ij} x_j(t) - \sum_{j,k=1}^{N_I} a_{jk} x_j(t) x_k(t) \right) \quad (1)$$

$$\sum_{i=1}^{N_I} x_i(t) = 1 \quad (0 \leq x_i(t) \leq 1). \quad (2)$$

These equations, the *replicator equations*, are generally used to describe the evolution of self-replicating entities,

so-called replicators [17]. The equations are also termed the *game dynamical equations* in the game theory. Moreover, they are equivalent to the $N_I - 1$ dimensional Lotka-Volterra equations [16]. Therefore, we will use the term *species* when referring to replicators hereafter. The variable x_i denotes the *population density* of the species i . N_I denotes the initial number of species, that is, the initial value of the diversity. The (i, j) -th element of the matrix $A = (a_{ij})$ determines the effect of species j on the growth rate of species i . Here we use $a_{ii} = -1$ for intraspecies interaction coefficients and assign the interspecies ones a_{ij} ($i \neq j$) as time-independent Gaussian random numbers with mean 0 and variance v . This assumption of random interactions is based on the hypothesis that a biotic fusion reorganizes species relationships in a random fashion [11]. This kind of ecosystem with random interaction also can be produced by the so-called *species-area effect* that paleontologists have asserted to be a trigger of mass extinction [18]. For example, because the species-area effect may be caused by declining sea levels, which confines many biologically-isolated species to a narrow area, drives them into competition and, eventually, brings biotic fusion. We also believe that the random interaction model is important as a first step of understanding the behavior of a large ecosystem with many species interacting in a complex way. For such a random interaction model, the local stability condition has been clarified [12–14] in the $N_I \rightarrow \infty$ limit. However, the global behavior is hardly treated analytically, because the equations are highly nonlinear and the dynamics often shows complex behavior, such as *heteroclinic orbits* [19,20] or *chaos* [21,22], even at a small degree of freedom ($N_I \geq 4$).

Here we should note that extinction is not well-defined in the above model with a large N_I because of the heteroclinic orbits. The reason is that even though a heteroclinic orbit approaches a *saddle* where some species are extinct, the population densities never reach exactly zero and the orbit eventually leaves for another saddle where the population densities revive. Moreover, this transition among saddles continues cyclically or chaotically. In this sense, heteroclinic orbits have never been believed to be biologically significant.

Considering the above problem, we introduce a parameter δ , the extinction threshold, to the dynamics (1)-(2) : at each discrete time step, the population density x_k is

set to zero if this quantity becomes less than δ . The population densities of the surviving species $\{x_i\}$ ($i \neq k$) are then renormalized to satisfy $\sum_{i \neq k} x_i = 1$. This renormalization implies that the niche of an extinct species is divided among the survivors. The diversity decreases through the above process, and we denote its value by N . Thus, the present model can be interpreted as a dynamical system whose degree of freedom is a time-dependent variable. Although this time-dependent degree of freedom is inevitable not only in population dynamics [23,24] but also in many fields, such a highly non-linear model has never been systematically analyzed.

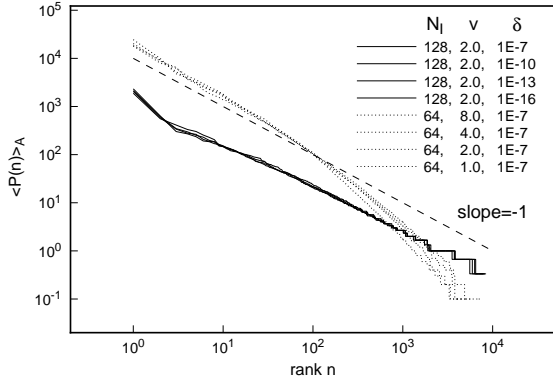


FIG. 1. Basin-size distributions for (a) $N_I = 64$ sampled from 100000 initial states and averaged over 10 samples of A , (b) $N_I = 128$ from 20000 initial states and 3 samples of A .

Whenever given a set of parameters A , δ and the initial diversity $N_I \equiv N(t=0)$, the initial state $\{x_i(0)\}$ evolves until a steady state is achieved. In this state extinction no longer occurs, and there remains a stable subecosystem with a comparatively small number of surviving species (*core species*) $N_F (\leq N_I)$. In this state, although almost all orbits converge to an equilibrium point, we also find periodic orbits. Chaotic orbits are very rare. Heteroclinic orbits are never achieved because the existence of the finite δ prohibits any orbit from approaching a saddle.

This introduction of δ also introduces a finite size effect into the replicator equations, because δ coincides with a minimum unit of reproduction of each species, and its reciprocal $1/\delta$ corresponds to the permissible population size of the ecosystem. Let us refer to this kind of dynamics as *extinction dynamics* (ED). By the series of extensive numerical simulations, we investigate novel features of ED, especially the dependence of ED on three parameters: N_I , v and δ .

From the view point on the random system theory, it is important to observe a typical behavior of ED by executing *random average* of quantities over samples of a random matrix A . Hereafter, we will in general write this average as $\langle \dots \rangle_A$.

The first result of this Letter concerns basin-size distribution of ED which has a large number of basins of attraction. Here, we identify each ‘attractor’ only by com-

position of core species, not by its trajectory. In other words, even if there coexist more than one isolated attractor in a system of core species, we do not discriminate these attractors and we regard them to be in one basin of ‘attraction’. The reason is that in ED such coexistence is rare and this classification of basins of attraction also agrees with a classification of subecosystems appearing by ED.

In order to obtain the basin-size distribution, we (a) iterate ED starting from a sufficient number of random initial states in a system with same parameters and a same random matrix A , (b) count basin size as the number of initial states which converge to each ‘attractor’, and (c) make a rank-size distribution $S(n)$, where the natural number n denotes the rank of each basin and can reach the total number of ‘attractors’ found in the simulation. Moreover, the above process is iterated for a sufficient number of random matrices A with same v and we finally obtain a basin-size distribution $\langle S(n) \rangle_A$ for a parameter set. $\langle S(n) \rangle_A$ ’s for various parameter sets are shown in Fig. 1.

We can see the significant characteristic that $\langle S(n) \rangle_A$ follows the power law. This indicates that the phase space of ED is divided in such a way that the size of each basin of attraction resembles each term of a geometric series. Moreover, each exponent of the power depends only on N_I , not on δ nor v . The independence of δ strongly suggests that the basin-size distribution of the original replicator equations (ED in the limit $\delta \rightarrow 0$) also follows the power law. This conjecture is relevant to the hierarchal coexistence of infinitely many attractors in the replicator equations [25]. The power law of rank-size relationship with exponent near unity is often referred to as Zipf’s law [26], known in linguistics and diverse fields.

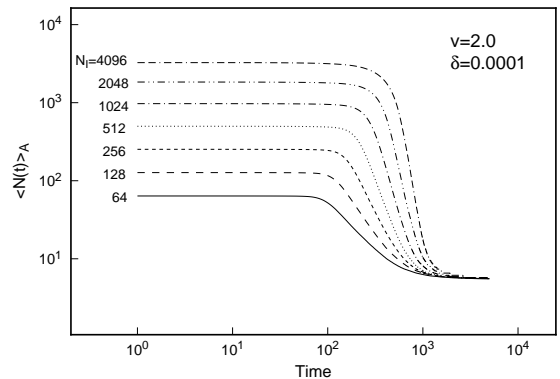


FIG. 2. Extinction curves for various values of N_I with $\delta = 0.0001$ and $v = 2.0$. Each curve represents an average taken over 1000 samples of A .

Figure 2 shows the second result of this Letter: average diversity as a function of time, $\langle N(t) \rangle_A$ (*the extinction curve*). Two significant characteristics can be seen from this figure. First, the average final diversity $\langle N_F \rangle_A$ is independent of N_I . This result implies that no matter

how large the diversity of initial species, the average diversity of species in the final state is small in comparison. That is $N_F \ll N_I$. In other words, when a large random ecosystem emerges as a result of biotic fusion, a mass extinction of ‘size’ $N_I - \langle N_F \rangle_A$ will occur. Secondly, the avalanche of mass extinction begins after some *induction time* [27] t_I , and ends in each case at nearly the same time $t_R \sim 10^3 (\geq t_I)$. As N_I becomes larger, t_I also becomes larger and approaches t_R . Therefore, for sufficiently large N_I , the extinction curve shows a sharp drop at t_I . Such an abrupt mass extinction occurring on a short time scale is highly relevant to the notion of *punctuated equilibria* [28].

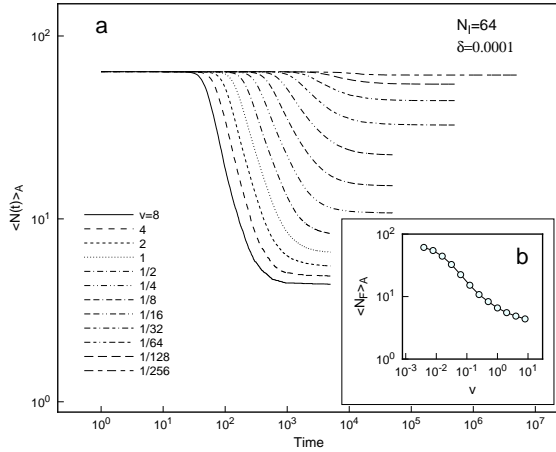


FIG. 3. (a) Extinction curves for various values of v with $N_I = 64$ and $\delta = 0.0001$, averaged over 1000 samples of A . (b) The average diversity of core species $\langle N_F \rangle_A$ as a function of v . In the limit $v \rightarrow 0$, $\langle N_F \rangle_A \rightarrow N_I$, because this is the limit of no interspecies interaction ($a_{ij} = 0$), and in this limit the right hand side of Equation (1) becomes 0.

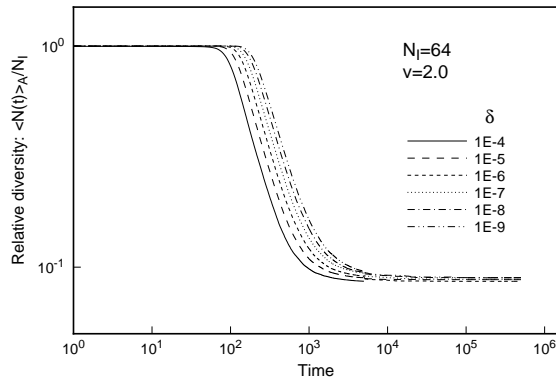


FIG. 4. Extinction curves for various values of δ with $N_I = 64$ and $v = 2.0$, averaged over 1000 samples of A .

Figure 3 concerns variation of extinction curves with v . As v becomes larger, the induction time t_I becomes shorter (Fig. 3a), and $\langle N_F \rangle_A$ becomes smaller (Fig. 3b). Consequently, when the order of the interspecies inter-

action coefficients becomes large compared with the absolute value of the intraspecies ones ($\{a_{ii} = -1\}$), the avalanche of mass extinction begins earlier, and a smaller diversity of species survives. Extinction curves for several values of δ are also shown in Fig. 4. From figures 2, 3 and 4, we can conclude that $\langle N_F \rangle_A$ depends only on v , but not on N_I nor δ , which contrasts the parameter dependence of $\langle S(n) \rangle_A$ only on N_I .

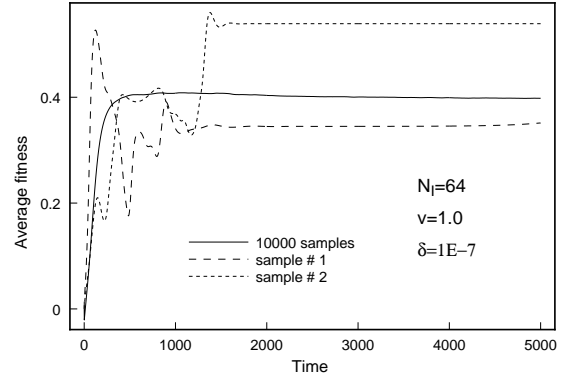


FIG. 5. Time development of $\langle \tilde{f}(t) \rangle_A$ over 1000 samples of A with $N_I = 64$, $v = 2.0$ and $\delta = 10^{-7}$. Two samples of average fitness $\tilde{f}(t)$ are also depicted as dotted curves

Here we also mention the time development of the *average fitness* $\tilde{f}(t) \equiv \sum_{i=1}^N \sum_{j=1}^N a_{ij} x_i(t) x_j(t)$ and its random average $\langle \tilde{f}(t) \rangle_A$. They are depicted in Fig. 5. It should be noted that the average fitness takes on positive values, except during the short period in the beginning. The final value of $\tilde{f} \sim 0.4$ is higher than the standard deviation $\sigma \sim 0.16$ of average fitness which is expected for a randomly generated ecosystem with same diversity ($N_F \sim 8$). Thus, more stable ecosystems are self-organized by ED. We also observe that $\langle \tilde{f}(t) \rangle_A$ does not show monotonic increase and reaches maximum value at the time near t_I . It suggests that, in general, the average fitness shoots up by the avalanche of extinction of low fitness species around the induction time and settles down to the final value via competition among core species.

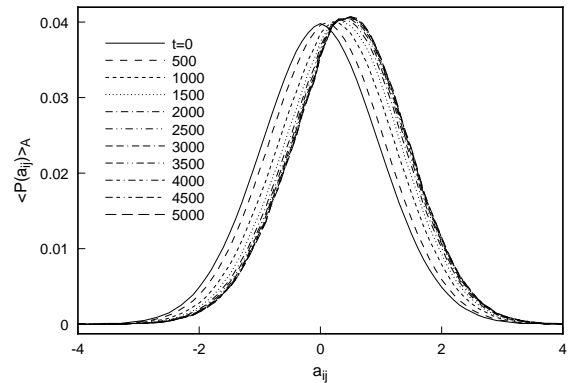


FIG. 6. Snap shots of interaction coefficients distribution averaged over 2000 samples of A with $N_I = 64$, $v = 2.0$ and $\delta = 10^{-7}$.

Time development of distribution of interspecies interaction coefficients a_{ij} ($i \neq j$) among surviving species is depicted in Fig. 6. The average of a_{ij} shifts to positive value along the time, which means that the relationship among the species becomes cooperative by ED. This also contributes the increase of average fitness. It should be noted that the distribution continuously holds its shape of gauss distribution. Therefore, the interspecies interaction coefficients of core species are still random, and various types of relationship among core species are realized by ED.

In this Letter, we ignore any effects by immigrants or invaders, which increase diversity, and we focus on global biotic fusion where no species ever comes from outside. Moreover, we do not consider any mutants because avalanche of mass extinction occurs so quickly that any evolution of mutants never follows. By neglecting these effects, the nature of extinction on rather short time scale is exclusively clarified. However, by introducing the effect of the increasing diversity, we can study the nature of ED on much larger time scale. For example, it must be interesting problem whether ED shows the self-organized criticality [8,29].

The present theory suggests that a biotic fusion by some external shock will cause a mass extinction if the fusion occurs in large scale and the interspecies interactions become random. It also can be a mathematical biological foundation of the species-area effect because it possibly plays a similar role like the biotic fusion. Furthermore, our results clarify the importance of the extinction threshold, i.e., the finite size effect for the replicator equations.

Finally, we strongly believe in the universality of our model, consisting of replicator equations and the finite size effect, because the former are accepted models in many scientific fields, such as sociobiology, prebiotic evolution of macromolecules, mathematical ecology, population genetics, game theory and even economics, and the existence of the latter is inevitable for such fields.

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- * E-mail address: tokita@paradox.harvard.edu; Permanent Address: Condensed Matter Theory Group, Graduate School of Science, Osaka University, Toyonaka 660, JAPAN
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